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Mesquite recruitment in the Chihuahuan Desert: Historic and prehistoric patterns with long-term impacts

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Abstract

Mesquite (*Prosopis glandulosa*) has increased in dominance over large areas of the Chihuahuan Desert, chiefly at the expense of once expansive desert grasslands. Excessive grazing and seed dissemination by livestock are often cited as the cause of this transition. We propose an alternate hypothesis that expansion of mesquite is not simply due to cause and effect relationships during recent history; rather, mesquite expansion is a result of a series of cause and effect relationships that transpired over a much longer timeframe (millennia). We assert that mesquite expansion may have ultimately occurred in the absence of widespread livestock grazing during the last 130 years because of removal of barriers to mesquite expansion created by indigenous peoples. We explore factors that attenuate or intensify mesquite expansion, and examine how a series of fine scale, but temporally seminal, events can propagate across multiple scales. Furthermore, we examine the relevance of this hypothesis for present day remediation of shrub-dominated grasslands and conclude that knowledge of historic and prehistoric events and processes are critical to effectively manage landscapes.

Keywords: Historic legacy; Invasive species; Landscape history; *Prosopis glandulosa*; Seed dispersal

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1. Introduction

Desertification is widespread throughout arid and semi-arid regions of the world (United Nations Environmental Programme, 1997). In the Chihuahuan Desert, desertification is characterized by a loss of grasslands as shrubs increase in dominance. Accompanying this transition is a substantial loss in livestock productivity when shrubs replace palatable grasses. In addition, wind and water erosion become dominant factors in shaping the landscape. Erosion alters soil fertility and hydrological patterns in ways that compromise the productive potential of the region to meet human needs for extended periods. This transition is often viewed as irreversible, requiring significant economic and biological inputs in order to return the landscape to a grassland state. Causes of desertification in the Chihuahuan Desert are believed to be due to a combination of factors, including (1) livestock grazing, (2) fire suppression, and (3) climatic change (Grover and Musick, 1990). In the case of mesquite (*Prosopis glandulosa*), a dominant Chihuahuan Desert shrub, seed dispersal by livestock is considered to be a primary cause of conversion from grassland to desert scrub (Buffington and Herbel, 1965; Norris, 1950). One event commonly viewed as having initiated this change is the arrival of large beef cattle herds from the eastern United States during the 1880s (Fredrickson et al., 1998). However, understanding the evolution of mesquite may provide insight into the processes of mesquite encroachment and may have profound management implications.

Peters and Havstad (2006) identify five key elements that connect spatial units across scales. Two of these are transport processes and historical legacy. Our first objective is to examine the role of seed dispersal as a key transport process in the expansion of mesquite in the northern Chihuahuan Desert. We propose that this transition from grassland to mesquite shrubland was not a single cause and effect relationship, but was probably initiated by several factors, some which predate the 1880s (i.e. historical legacy; see Peters and Havstad, 2006). Our second objective is to examine the role of seed dispersal in remediation and identify opportunities to improve the effectiveness of efforts to reduce mesquite dominance and promote desert grasslands.

2. Prehistoric mesquite expansion dynamics

Mesquite likely evolved with the Pleistocene megafauna of North America. Long et al. (1974) reported that mesquite seeds were present in the desiccated dung of the Shasta ground sloth, providing strong evidence of mesquite co-evolution with Pleistocene megafauna. Seeds were probably consumed and dispersed by other animals, such as camelids, hippopotamus or rhinoceros sized notoungulates, and elephant-like stegomastadons (see Mehringer, 1967). Within its range, mesquite may have exhibited a similar ecological role to species of acacia (a close relative of mesquite in the *Fabaceae*) in the current Serengeti-Mara ecosystem of Africa. In that system, the prevalence of acacia woodlands closely follows both elephant populations and incidence of fire. After the Rinderpest epidemic of the 1890s, both human and elephant populations were low, with elephant populations further reduced by ivory poachers (Dublin, 1995). During the following 30–50 years, dense acacia thickets were established which provided habitat for tsetse flies. With ungulate populations remaining low due to Rhinderpest and above normal rainfall during the 1960s, sufficient fuel was present to carry extensive fires that caused a significant decline in acacia woodlands. Fires were typically started by humans to improve hunting and reduce tsetse fly habitat. Woodlands were also impacted by the compression of elephant populations as they were moved into preserves to make way for expanding human populations (Gillson and Lindsay, 2003) because elephants browse young trees and maintain a grassland state. Western (1997) stated that in Amboseli, Kenya, "you see herds of cattle filing into the park to graze, passing elephants headed out to browse. With elephants and cattle transforming the habitat in ways inimical to themselves but beneficial to each other, they create an unstable interplay, advancing and retreating around each other like phantom dancers in a languid ecological minuet playing continuously over decades and centuries. Habitats oscillate in space like a humming top, driving and being driven by climate, animals and people." A scenario similar to that described by Dublin (1995) and Western (1997) is plausible for mesquite/megafauna interactions during the Pleistocene, possibly resulting in a dynamic fluctuating between grassland and shrubland states.

One constraint to the Mara-Serengeti comparison may be the limited effectiveness of fire to reduce mesquite dominance. Even with low ungulate populations and sufficient rainfall to provide fuel, fire frequency and intensity must be sufficient to prevent recruitment of young plants because mature plants generally resprout after fire (Wright, 1971, 1980). If associated grasses were similar to the upland black grama (*Bouteloua eriopoda*)/dropseeds (*Sporobulus spp.*) association present today, then frequent fires would result in a loss of grasses and increased bare erodible soil. The ability of mesquite to resprout is a possible adaptation to herbivory and/or fire, while the presence of spines on mesquite is a likely adaptation to herbivory due to long-term co-evolution with browsers. Rohner and Ward (1997) reported a similar adaptation for closely allied species. It is these adaptations during the Pleistocene, or possibly earlier, that might affect mesquite's later role in Chihuahuan Desert ecosystems.

Where it occurred, the mesquite/megafauna interaction in North America may have been disrupted by human invasion. While controversial, the preponderance of evidence indicates that Eurasian immigration into North America led to anthropogenic extinction of Pleistocene megafauna between 11.5 and 10 thousand years ago (Alroy, 2001; Barnosky et al., 2004). Loss of Pleistocene megafauna, in conjunction with the warming post-glacial climate, almost certainly altered mesquite dynamics. The combination of increasing aridity and lack of large browsers may have led to an increase in mesquite between 10 and 6 thousand years ago that is consistent with an apparent increase in C_3 shrubs for this period (Monger, 2003; Fig. 1). Based on packrat middens (Van Devender, 1990), mesquite occurred sporadically during the middle and late Wisconsin glaciations in the northern Chihuahuan Desert. In the Big Bend region (western Texas, USA, elevation 580 m, 29°N, 102°W), mesquite was absent 10,500 years ago but common about 9000 years ago. Mesquite was not common north of that area (Hueco Tanks; near El Paso, Texas, USA, elevation 1360 m, 31°N, 106°W) until 8000 years ago, suggesting that climate was a dominant factor affecting the expansion of mesquite at regional scales. Within this scale, animal dispersal probably influenced mesquite-infilling, while the absence large browsers meant there was little to impede its movement at this scale.

Over time, humans began to influence mesquite dynamics more directly as they too became both a seed predator and a dispersal agent. For pre-European peoples of the southwestern United States, dependence on mesquite was extensive; mesquite was incorporated into almost every aspect of their lives. Mesquite was a primary source of food (Bell and Castetter, 1937; Felger, 1977). In some cultures, mesquite beans were

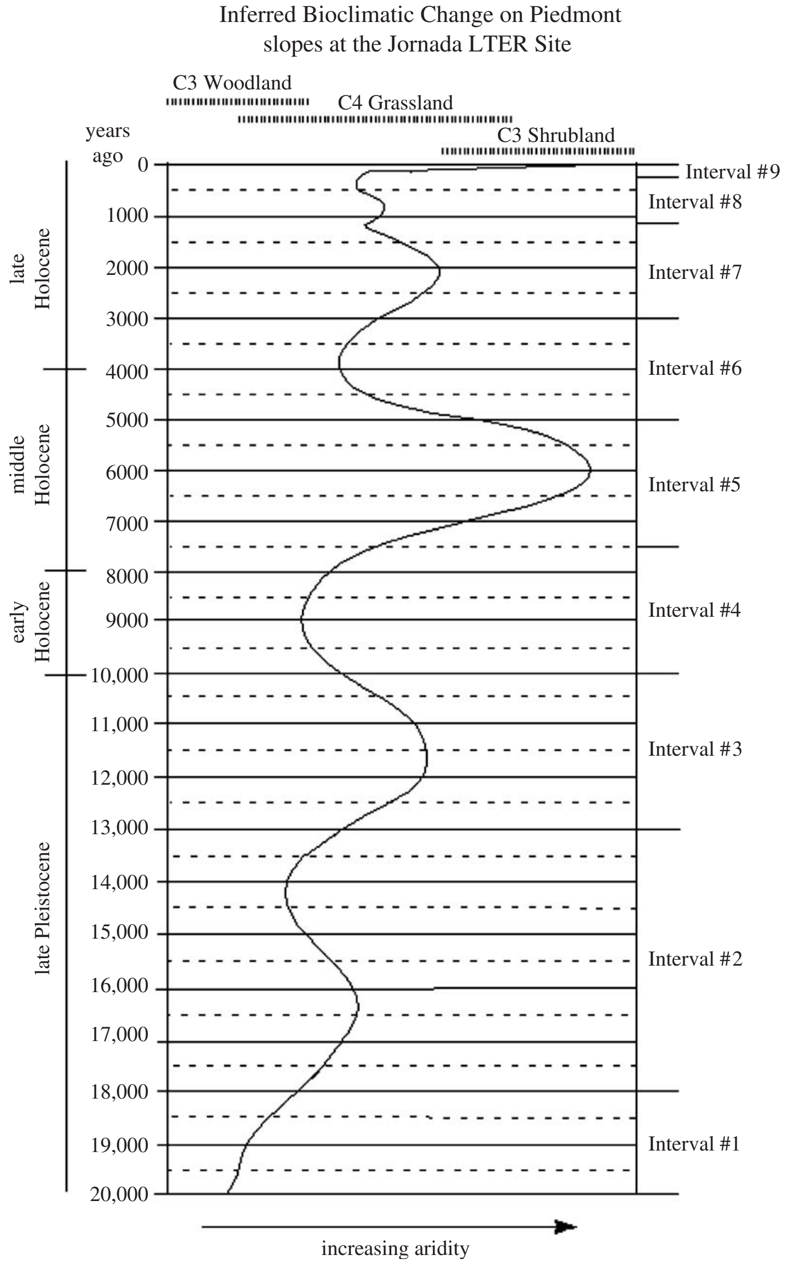

Fig. 1. Inferred bioclimatic changes over the past 20,000 years on piedmont slopes of the Jornada Basin Long-Term Ecological Research site in southern New Mexico (from Monger, 2003).

harvested from early July until late August. According to Spier (1933; as cited by Bell and Castetter, 1937), "Women went out in groups and several men usually accompanied them as protection. Gathering proceeded day after day until the bushes held no more, for mesquite was their staple.'' Mesquite was also a source of fuel, medicine, building material, cosmetics, and the subject of religious ritual. Felger (1977) also stated that mesquite was ''a staff of life of the arid regions of the arid southwestern North America.'' Mesquite was treated as a commodity to the extent that individual bushes were owned and identified as to their owner. Some peoples robbed packrat nests of mesquite beans, and during times of scarcity, mesquite was a trade item (Felger, 1977). The ultimate effect of heavy use by humans was probably to limit seed dispersal by mesquite and thus restrict dispersal and eventual dominance of mesquite. Use of mesquite for fuel, weaponry, and building material certainly exerted a negative pressure on the expansion of regional mesquite populations, while trade likely served to disperse mesquite and blend mesquite ecotypes. Factors that affected human populations probably inversely affected mesquite. The human population in North America declined steadily between 1500 and the early 1900s (Ubelaker, 1992). Estimates of the North American Indian population size in the Southwest culture area indicate a decline from over 450,000 in 1500 to a less than 160,000 in 1900 (Table 1).

In addition to direct effects, pre-European humans undoubtedly exercised indirect controls over mesquite distribution patterns. Primary among these indirect controls was hunting. As was the case in northern environments (Martin and Szuter, 1999), settlement patterns of indigenous peoples may have greatly influenced game abundance in the southwestern United States. The net effect of hunting is a reduction of mammalian populations near settlements. It has been shown that even under relatively low human population densities, distance to human settlement and settlement density can have an impact on wildlife distribution and abundance (Laliberte and Ripple, 2003). Mammals both prey on seedlings and disperse seed; consequently, survival of seedlings may have increased due to the effect of hunting, but seed dispersal distance probably decreased.

York and Dick-Peddie (1969) provided further evidence that mesquite distribution was influenced by earlier human populations. Based on 1858 land surveys, mesquite distribution on the Jornada de Muerto basin and areas surrounding Las Cruces, New Mexico was largely limited to areas known to be indigenous settlements (York and Dick-Peddie, 1969). In areas less favorable for human habitation, human control over mesquite patterns on the landscape was probably minimal, yet may have contributed to regional variation in mesquite density.

Table 1
Estimates of North American Indian population size in the Southwest culture area[a]

Year	Population
1500	454,200
1600	420,000
1700	276,260
1800	215,950
1850	176,740
1900	158,283
1925	180,010

[a]From Ubelaker (1988).

3. Historic mesquite expansion dynamics

With the arrival of European peoples in the early 1600s, the negative feedbacks exerted on mesquite distribution by pre-European peoples began to wane. In the arid southwest, people were aggregated around Catholic missions and their diets shifted from mesquite to wheat (Felger, 1977). European diseases reduced indigenous populations, while the reintroduction of the horse likely destabilized the balance of power among indigenous nations (Fredrickson et al., 1998). Furthermore, the introduction of sheep and cattle provided an alternate food source, further reducing dependence on mesquite beans in the diet. The influence of indigenous peoples on mesquite dynamics was further reduced by warfare and treaty. The often-constraining influence of human activities on mesquite populations was reduced by these events and mesquite dominance began to expand. Within its range, seed dispersal distances and subsequent seedling establishment then probably limited mesquite expansion.

Intact mesquite seeds are found in the scat of coyotes (*Canis latrans*), jackrabbits (*Lepus californicus*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocarpra americana*) (Fisher, 1950; E.L. Fredrickson, personal observation). The importance of mesquite seed in the diet of these animals is likely to increase during drought years when other food sources are limited. Interestingly, it is during dry periods that mesquite is most prolific, since flowering and seed production are greatest during periods with low soil water and least with ample soil moisture (Lee and Felker, 1992; Mooney et al., 1977). As a result, seed dispersal is likely to be greatest during drought. Populations of potential seedling predators such as small mammals are reduced by limited food availability during drought, with population decline related to drought length. Also, drought kills grasses that can compete with mesquite seedlings (Glendening and Paulsen, 1955), thus opening sites conducive to seedling establishment. With onset of summer rainfall at the end of a drought, mesquite seedlings may have both a lower probability of damage from herbivores and reduced competition from grasses.

We hypothesize that without the pressure of pre-European peoples, mesquite began to expand, with pre-European settlements providing a foci for most of this expansion. Expansion likely occurred in pulses with greatest establishment following periods of drought. Introduced livestock became a new vector for dispersal of viable seeds. In feeding trials with horses, cattle, and sheep fed mesquite beans, 91%, 79%, and 16%, respectively, passed through the digestive tract intact (Fisher et al., 1959). Haas et al. (1973) reported germination rates of 82%, 69%, and 25% for seeds passing through horses, cattle and sheep, respectively. Prior to introduction of large herds of cattle during the 1880s, the effects of livestock dispersal were primarily limited to areas surrounding European settlements or along roads, as livestock movements were generally restricted by lack of surface water. Roads such as the "Camino Real de Tierra Adentro" traveling through the Jornada del Muerto basin are now visible in aerial photographs by the dense mesquite along the route, presumably from seed dispersed by livestock (Peters et al., 2006). Another example of mesquite dispersal by livestock is illustrated in Fig. 2, which depicts shrub cover changes from 1937 to 2003 within a pasture in the Jornada del Muerto basin. Aerial photographs and image processing techniques were used to estimate percentage shrub cover, which increased from 0.9% in 1937 to 13.1% in 2003 (Laliberte et al., 2004). The lines visible from southwest to northeast are old livestock trails that are darkened because of mesquite from livestock-dispersed seeds and/or conditions favoring their germination

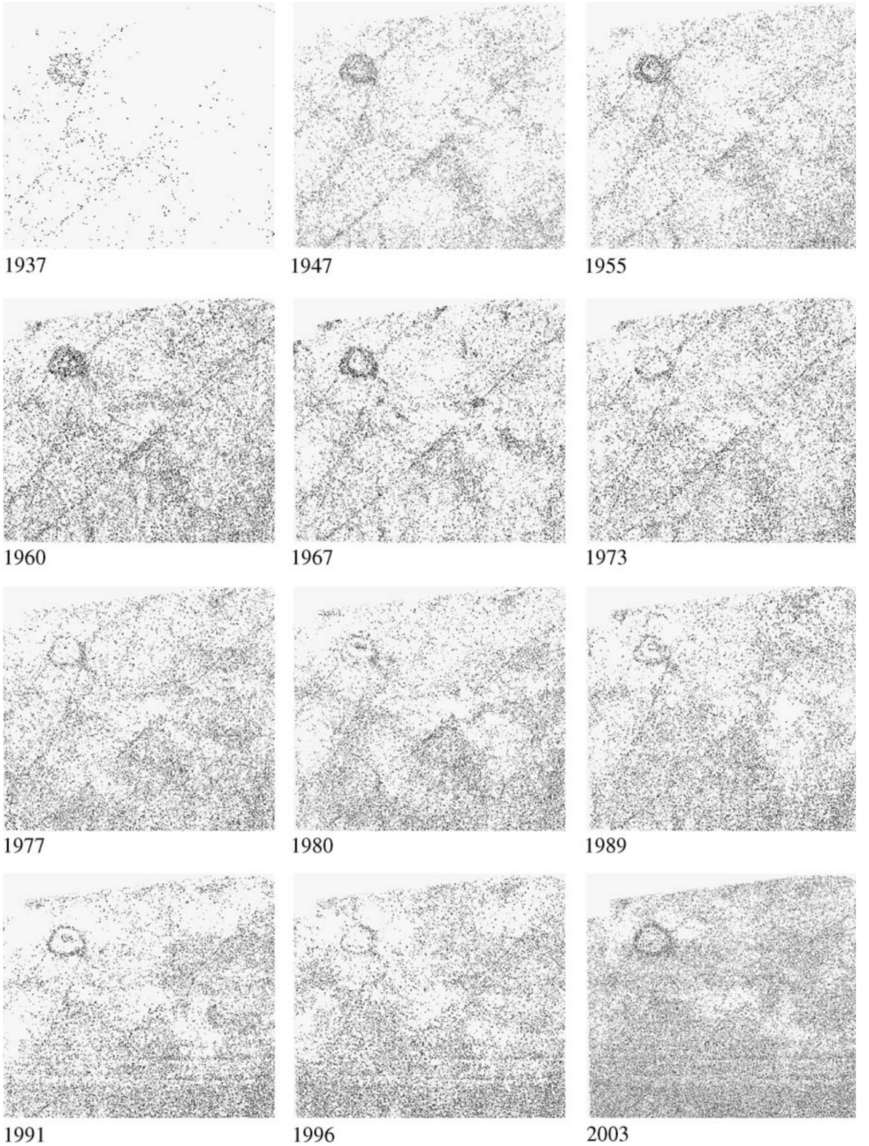

Fig. 2. Changes in shrub cover for a pasture in the Jornada Basis between 1937 and 2003, based on image processing of aerial photography. Distinct lines running southwest to northeast are old livestock trails that appear dark due to mesquite shrubs most likely from seeds dispersed by livestock.

and survival. Although lines appear to become less distinct over time, the shrubs did not actually disappear; rather, other shrubs filled in around the original plants, causing lines to appear less distinct in more recent years.

Without negative feedbacks from Pleistocene megafauna or indigenous peoples, mesquite expansion was likely to occur logarithmically and increase with each episodic drought. However, another event occurred during this timeframe that further accelerated mesquite expansion. Due to speculative eastern markets and a series of severe winters in the Great Plains, livestock numbers swelled precipitously in the desert southwest during the mid to late 1880s (Fredrickson et al., 1998; Havstad et al., 2006; Stoddart et al., 1975). In addition to increased seed dispersal associated with excessive livestock numbers, overgrazing provided open sites conducive to mesquite establishment. During World War I, overgrazing was sustained and even amplified to assist the war effort (Fredrickson et al., 1998). Also during this time, large campaigns were initiated to exterminate rodents thought to compete with livestock for forage (Oakes, 2000; Jornada Experimental Range archives), which effectively reduced seedling predators. No longer was mesquite expansion limited to post-drought conditions. Complete mesquite dominance throughout its potential range in the Chihuahuan Desert grasslands might have taken centuries to manifest, but with the arrival of very large herds of livestock, the conversion took place in less than 100 years.

4. Role of seed dispersal in remediation

In response to excessive shrub invasion and grassland degradation, research was initiated by universities and federal institutions in the early to mid 1900s to develop grazing practices that prevent rangeland degradation in the arid southwest. These practices, while helpful, largely ignored livestock dispersal of mesquite seed and thus often resulted in failure. Furthermore, even with complete livestock removal, the stage had been set because widespread seed dispersal had already occurred. The inability of cattle exclosures constructed during the 1930s to inhibit mesquite expansion supports this statement (Peters et al., 2006). Mesquite expansion was inevitable in the absence of forces that negatively affect it (e.g. megafauna, indigenous peoples).

Prior to development of state and transition models, predicting a return to grasslands would not be possible without some form of intervention (Bestelmeyer et al., 2003). Range ecologists were frantically seeking ways to reduce the "threat" of mesquite using an assortment of technologies (Herbel et al., 1983; Kreuter et al., 2001; Wright et al., 1976). Based on observations of mesquite control efforts in the Jornada del Muerto basin, these practices cannot be viewed as economically feasible in Chihuahuan Desert conditions due to the short lifespan of these treatments, which generally persist less than 20–30 years (Gibbens et al., 1992). This interval is insufficient in terms of increased forage yield to pay for most treatments. Most of the treatments examined did not attempt to control for seed dispersal either by cattle or native mammals, nor did they account for seed bank dynamics and the presence of mesquite seed. Controlling for these factors should extend the life of these treatments and improve the economics of mesquite control efforts. Others suggest that "re-wilding" of the northern Chihuahuan Desert using modern day surrogates of the Pleistocene megafauna may be used to control shrubs like mesquite (Donlan et al., 2005). However, due to changes that have occurred during the past 10,000 years or more, disturbance resulting from implementation of this strategy may cause irreversible damage that could propagate across northern Chihuahuan Desert landscapes. We suggest that the diverse uses of mesquite by indigenous people may have limited its spread in the northern Chihuahuan Desert and that future control of mesquite may also arise from our appreciation of its attributes and the eventual use of mesquite to meet human needs.

5. Conclusions

The historic legacy is a key element that contributes to the spatial and temporal heterogeneity observed in arid and semi-arid landscapes (Peters and Havstad, 2006). Based on the legacy of the Chihuahuan Desert, it appears that a grassland state can only be obtained if an active force is used that negatively impacts mesquite populations. Simultaneously, there is a need to reduce anthropogenic factors promoting mesquite dominance. Historically, indigenous peoples and Pleistocene megafauna used mesquite as a resource and by doing so, exerted significant pressures on mesquite populations that apparently limited or reduced mesquite expansion and dominance. Currently, few forces are in place that create this effect. Furthermore, today's livestock management practices promote mesquite dominance via seed dispersal. However, even with immediate removal of livestock, mesquite would likely increase in dominance unless some measure of sustained control is attained through time. Since the Pleistocene, conditions have changed sufficiently to prevent introduction of animals that simulate Pleistocene megafauna. In addition, current economic conditions have eliminated the use of mesquite in a similar manner as pre-European peoples. We have entered a yet another era in the eventual history of mesquite. If desert grasslands are desired, then new and innovative measures must be undertaken. These measures will be more successful if they take into account the life history traits of mesquite that have been revealed by the legacy of its response to changing environmental conditions.

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